Reproductive biology of round sardinella (Sardinella aurita) in the north-eastern Mediterranean

ATHANASSIOS C. TSIKLIRAS and EFTHIMIA ANTONOPOULOU
Aristotle University of Thessaloniki, School of Biology, Department of Zoology, Laboratory of Animal Physiology, UPB 134, 541 24, Thessaloniki, Greece. E-mail: atsik@bio.auth.gr

SUMMARY: The reproductive biology of round sardinella, Sardinella aurita Valenciennes, 1847, was studied for the first time in the north-eastern Mediterranean Sea. Round sardinella has gained much attention lately because of its biomass increase, which might be the result of climatic changes occurring across the Mediterranean Sea. Monthly samples were collected on board commercial purse-seiners for two complete year cycles (September 2000 to August 2002). Round sardinella is a gonochoristic fish. The overall female to male ratio was not statistically different (P=0.34) from unity, although it varied monthly and with the length of the fish. The seasonal changes in the gonadosomatic index and the macroscopic characteristics of gonads showed that round sardinella in the northern Aegean spawns between May and July. Male round sardinella reach first sexual maturity at a smaller total length than females (155.0 and 168.3 mm respectively). Mean absolute fecundity (FA) increased exponentially with body length (FA=0.0949×L^{4.22}) and weight (FA=511.19×W^{1.02}), with an average of ~21,000 oocytes produced per spawning female. Relative fecundity (FR) ranged between 242 and 681 oocytes/g of body weight (average: 445 oocytes/g). The frequency distribution of oocytes showed that round sardinella produces a single batch of oocytes. In general, the reproductive characteristics of round sardinella in the north-eastern Mediterranean Sea differed when compared to stocks from other areas of its distribution.

Keywords: sex-ratio, maturity, fecundity, spawning, round sardinella, Aegean, Mediterranean.

INTRODUCTION

Fish have developed reproductive strategies and traits that ensure the survival of the species under variable and often unfavourable conditions (Potts and Wootton, 1984). The reproductive strategy of each species is expressed by certain characteristics such as age and size fecundity, time duration and frequency of spawning, size at first maturity and reproductive behaviour (Potts and Wootton, 1984;
Wootton, 1998). All these characteristics are useful for managing fisheries (Jennings et al., 2001), particularly for single species pelagic fisheries.

Round sardinella, *Sardinella aurita* Valenciennes, 1847 (Pisces, Clupeidae), is a widely distributed, middle-sized pelagic fish. The distribution of the species is tropical and subtropical often associated with major upwelling systems (Durand et al., 1998; Froese and Pauly, 2003, www.fishbase.org). Its range extends to the western and eastern Atlantic Ocean, the Pacific Ocean, the entire Mediterranean Sea and occasionally the Black Sea (Bauchot, 1987).

Round sardinella is a stenothermic and stenohaline species (Binet, 1982; Longhurst and Pauly, 1987; Fréon and Misund, 1999). Until about twenty years ago, it was only sporadically found in the northern Aegean Sea and its distribution was confined to the warmer and more saline southern Aegean waters (Ananiades, 1952). As a typical opportunistic species (Cury and Fontana, 1988), it has invaded the northern Aegean Sea waters over the last twenty years mainly due to climatic changes (Bethoux and Gentili, 1999). This is also the case in the Adriatic Sea (Kačić, 1984). However, an adaptation of the species to the local environmental conditions should not be excluded (Cury and Fontana, 1988).

The commercial exploitation of round sardinella in the Greek seas has steadily increased since the early 1990s (National Statistical Service of Hellas, 1990-2002) because it is in high demand by the canning industry and as bait for the profitable tuna and swordfish fisheries. Total landings increased from 69 t in 1990 to 2733 t in 2002. The main part of the landings is caught by the purse-seiners using light attraction (60-80%), while the remaining part is caught by small scale fisheries (i.e. netters, beach seiners and small ‘sardine-nets’) and bottom trawlers (Tsikliras, 2004a). Using pelagic trawls is prohibited in Greek waters.

The reproductive biology of round sardinella has been thoroughly studied in the western (Bakun and Parrish, 1990; Fréon et al., 1997) and eastern Atlantic (Fontana, 1969; Pham-Thuoc and Szypula, 1973; Cury and Fontana, 1988; Roy et al., 1989; Quaatey and Maravelias, 1999). In contrast, information is limited for the Mediterranean stocks and focused on the southern part of the sea. Size and age at maturity have been studied in Algerian (Bouaziz et al., 2001) and Tunisian waters (Gaamour et al., 1988) and Tunisian waters (Gaamour et al., 1988); and fecundity in Algerian (Bensahla Talet et al., 1988) and Tunisian waters (Gaamour et al., 2001). Data on its reproductive biology in Greek waters is very scarce (time and duration of spawning: Ananiades, 1952), which is the case for many eastern Mediterranean stocks (Stergiou et al., 1997).

The aim of the present study is to investigate the following aspects of the reproductive biology of round sardinella in the northern Aegean Sea: (a) the time and duration of the spawning season; (b) the annual reproductive cycle, in terms of seasonal changes in the gonadosomatic index and maturity stages; (c) the sex-ratio; (d) the size at first sexual maturity; and (e) the fecundity.

**MATERIAL AND METHODS**

Monthly samples were collected from Kavala Gulf (40°52′N, 24°25′E, northern Aegean, Greece) on board a professional boat using a commercial purse seine net (length: 800 m, height: 90 m and mesh size: 9 mm bar length) between September 2000 and August 2002 (Fig. 1). Each monthly sample consisted on average of 331 individuals (ranging between 212 and 549). Additional samples (906 individuals) were collected just prior to the spawning period of the species using an unselective gear (beach seine with...
cod-end mesh size of 8 mm, bar length), to avoid biased results taken with selective gear, which could give an inaccurate estimation of size at maturity (Jennings et al., 2001). The beach seine samples were only used for estimating size at maturity. Furthermore, sea surface temperature (SST, °C) was recorded monthly, using a CTD probe (Fig. 1).

Fish samples were immediately fixed on board in formaldehyde solution (8%, buffered) and were measured (total length, L, mm) and weighted (total weight, W, g) in the laboratory. Total length ranged between 97 and 243 mm for the males and between 102 and 248 mm for the females (monthly length frequency distribution is given by Tsikliras et al., 2005b). Gonad weight (GW) was recorded to the nearest 0.01 g. In overall, 7942 individuals were sexed and the maturity stages were determined using the six stage key of Nikolskii (1963). A $\chi^2$ goodness-of-fit test (Zar, 1999) was undertaken to compare the female:male (F:M) ratios (per month and within the size groups), with a hypothesized sex-ratio of 1:1. Sex and maturity stages were determined macroscopically.

The gonadosomatic index [GSI=(GW/W)×100] describes the relative size of gonads and is used as an index of reproductive activity (Wootton, 1998). Absolute fecundity ($F_a$) was determined in a sample of 105 gonads collected prior to spawning (stage V, Nikolskii, 1963) and preserved in Gilson’s fluid (Bagenal and Braun, 1978). Oocytes were counted volumetrically (Bagenal and Braun, 1978) and oocyte diameter was measured under a microscope. The relationship between $F_a$ and length or weight was described using the exponential equation: $F_a=ax^b$, which after a logarithmic transformation takes the form $\log F_a = \log a + b(\log x)$, where $x$ is either length or weight and $a, b$ are the regression constants. To assign equal weight to all size classes, mean $F_a$ per length class was used (Živkov and Petrova, 1993). Relative fecundity ($F_\%$) was considered as the number of eggs per unit of body weight (Nikolskii, 1963).

The logistic model is commonly used as a mathematical description of the relation between body size and sexual maturity (e.g. Echeverria, 1987). The length at which 50% of the individuals attained sexual maturity ($L_{50}$) was estimated by fitting a logistic curve to the relationship between the percentage of mature fish (P) and length class (L):

$$ P = \frac{e^{(v_1+v_2L)}}{1 + e^{(v_1+v_2L)}}, $$

and

$$ L_{50} = -\frac{v_1}{v_2}. $$

The proportion of mature fish for each 5 mm length class was estimated by sex and $v_1, v_2$ were calculated using the method described by Petrakis and Stergiou (1997), as adopted for maturity studies (Stergiou, 1999). For the estimation of $L_{50}$, mature individuals were considered those that were classified at stages IV to VI, while those classified at stages I to III were considered immature. A test for over-dispersion was performed by comparing the deviance statistic $\Delta$ to the $\chi^2$ distribution on N-2 degrees of freedom (Petrakis and Stergiou, 1997). The data are over-dispersed if $\Delta > \chi^2$. Finally, the age at 50% maturity and the dimensionless ratio $L_{50}/L_\infty$ (where $L_\infty$ is the asymptotic value of L), which expresses the proportion of the potential growth span of the species covered before maturation (Beverton, 1992), were calculated using the growth parameters previously estimated by Tsikliras et al. (2005b).

RESULTS

Sex-ratio

Round sardinella is a gonochoristic fish. External morphological and colour differentiation is not observed at any stage of its life cycle (monomorphism). In overall, 4014 (50.54%) out of the 7942 individuals sexed were females, and 3928 (49.46%) were males. The F:M ratio was 1.02:1 and did not differ significantly ($\chi^2=0.91$, $P=0.34$) from unity. Yet, the F:M ratio exhibited a monthly variation from 0.13 in June 2002 to 1.67 in December 2001. The size-specific sex-ratio showed that the number of males and females was equal for lengths lower than 160 mm, whereas the number of males was higher for length classes of 160 (F:M=0.43, $\chi^2=73.79$, $P<0.001$) and 170 mm (F:M=0.71, $\chi^2=27.39$, $P<0.001$). The sex-ratio did not differ statistically from unity for length classes of 180 (F:M=0.92, $\chi^2=1.85$, $P=0.179$) and 190 mm (F:M=0.96, $\chi^2=0.72$, $P=0.402$). Females generally dominated at lengths greater than 200 mm (Fig. 2).

Gonad weight

The weight of the testes ranged between 0.59 and 9.91 g (average 1.55 g, S.D.=0.81) for males with
length ranging between 159 and 243 mm. Similarly, the ovary weight ranged between 0.33 and 5.52 g (average 1.54, S.D.=0.88) for females with length ranging between 160 and 230 mm. Testes and ovaries accounted for 4.84% and 4.41% of the total weight respectively. An analysis of variance revealed the statistical difference in the average proportion of sexual organs to the fish body weight (F=5.32, P=0.021).

**Time of spawning and maturity stages**

The analysis of GSI indicated that the gonads of both sexes started to develop around April and matured fully a month later (Fig. 3a and b). Mean monthly SST (Fig. 3c) was 0.5 to 1°C higher during the first study year (mean: 18.15, range: 10.07-
27.41) compared to the second one (mean: 17.67, range: 9.62-26.51).

The spawning season of the species is confined to a specific period of the year and begins in May or June. Sexually mature individuals were only caught during May, June and July (Fig. 4). The first mature males and females (stages IV and V) appeared in April and May respectively. In June, almost all specimens of both sexes were mature and in July, 36.7% of males and 24.5% of females were spent (stage VI), while the rest were at stage II (Fig. 4). All individuals of both sexes were resting (stage II) between September and March with the exception of some immature (stage I) specimens caught in September and October 2001.

Size at maturity

The \( L_{50} \) was 155.0 mm for males and 168.3 for females (Fig. 5). The smallest mature male and female were 135 and 136 mm, respectively. All females with a length greater than 215 mm and all males with a length greater than 205 mm were mature. The parameters of the equations describing the relationship between the proportion of mature fish and length class are shown in Table 1. The \( L_{50}/L_{\infty} \) was 0.62 for males and 0.67 for females.

Fecundity and oocyte diameter

Absolute fecundity (\( F_A \)) exhibited high variability among females and ranged between 9,700 (S.D. of 4 subsamples=632) and 72,700 (S.D. of 4 subsamples=9,449) oocytes, corresponding to females with \( L=164 \) mm and \( L=228 \) mm respectively (mean=20,976, S.D.=7,741, n=105). Relative fecundity (\( F_R \)) ranged between 242 and 681 oocytes/g. An average of 445 (S.D.=98) oocytes/g was produced. Mean \( F_A \) increased exponentially with length and weight:

\[
F_A = 0.0949 \times L^{0.422}, \quad r^2 = 0.91, \quad P<0.01, \quad n=8 \text{ (Fig. 6a)}
\]

<table>
<thead>
<tr>
<th>Parameter estimates</th>
<th>Females</th>
<th>Males</th>
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<tr>
<td>Length range (mm)</td>
<td>129-230</td>
<td>125-243</td>
</tr>
<tr>
<td>( v_1 )</td>
<td>-10.10</td>
<td>-12.40</td>
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<tr>
<td>SE ( v_1 )</td>
<td>0.851</td>
<td>1.024</td>
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<tr>
<td>( L_{50} ) (mm)</td>
<td>168.33</td>
<td>155.00</td>
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<tr>
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<td>150.02</td>
<td>141.27</td>
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<tr>
<td>Upper 95 % CL ( L_{50} )</td>
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<td>168.73</td>
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<tr>
<td>Deviance statistic (( \chi^2 ))</td>
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<td>35.237</td>
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<tr>
<td>Degrees of freedom</td>
<td>19</td>
<td>23</td>
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<tr>
<td>( r^2 )</td>
<td>0.91</td>
<td>0.909</td>
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</table>

Based on the growth parameters of the species (Tsikliras et al., 2005b), the age at 50% maturity for males and females was 1.03 and 1.33 years respectively.

**Table 1.** Estimated mean length (\( L_{50} \), mm) and age (\( t_{50} \), yr) at which 50% of the fish are sexually mature and the parameters of the equations describing the logistic relationship between the proportion of mature fish (\( P \)) and body length (\( L \)) for male and female round sardinella, Aegean Sea.
In all stages of ovarian development, a permanent stock of oocytes smaller than 0.20 mm was observed. The average oocyte diameter just before spawning (oocytes $>0.20$ mm, stage V) was 0.44 (range: 0.20-0.76 mm, S.D.=0.05). There was no correlation between oocyte diameter and length ($r=0.056$, $P=0.55$). The unimodal frequency distribution of oocyte diameter showed that round sardinella is a determinate spawner producing a single batch of oocytes (Fig. 7).

DISCUSSION

Sex ratio

An overall balanced sex-ratio was found in the present study, which is in agreement with the results previously reported for round sardinella in Venezuelan waters (Fréon et al., 1997). In contrast, Boely and Champagnat (1970), and Gaamour et al. (2001) noted a female dominated population in Senegalese and Tunisian waters respectively. The differences in the size-specific sex-ratio were also reported for Libyan waters (Pawson and Giama, 1985) and were related to sexual differences in growth, mortality or energetic cost of reproduction. Females generally dominated the higher length classes in the northern Aegean, Algerian (Bensahla Talet et al., 1988) and Tunisian waters (Gaamour et al., 2001), while differences in the size-specific sex-ratios have been reported for other Mediterranean marine fishes (e.g. Stergiou et al., 1996).

Gonad weight

The testes frequently represent a much lower proportion of the total fish weight than the ovaries (Wootton, 1998). This sexual dimorphism, however, was not observed in round sardinella from the northern Aegean Sea. Moreover, the size of testes may relate to the mode of fertilization and the distance between the two sexes during spawning because external fertilization in the open sea requires greater amounts of sperm, and hence large testes, to ensure a higher rate of fertilization of the dispersed oocytes (Wootton, 1998). Additionally, the prespawning strategic behaviour of female round sardinella (Ben Yami, 1976) and other clupeoids (Blaxter and Hunter, 1982) may result in the dissemination of the two sexes and thus the need for larger sperm quantities than in other species. Male and female round sardinella in the northern Aegean Sea exhibited similar growth (and hence mortality) rates (Tsikliras et al., 2005b), indicating that the same pattern persists for their entire lifespan.

Time of spawning and maturity stages

The spawning of round sardinella in the northern Aegean occurs in one episode every year in early summer (May to July), according to the monthly variation of the GSI and the maturation stages of the fish.
As in most marine fishes, the time of spawning of round sardinella has evolved as a mechanism to ensure the synchronization of larvae appearance and the peak of primary production (i.e. the favourable conditions for offspring survival; Cushing, 1975; Blaxter and Hunter, 1982). However, the onset of the spawning season of round sardinella varied between the two study years probably owing to temperature differences, with GSI being positively correlated with temperature (Tsikliras, 2004b). The existence of a positive relationship between GSI and temperature does not necessarily imply a direct effect of temperature or an effect of temperature alone on the onset of spawning. Population-related changes and other factors such as food availability (e.g. Roy et al., 1989) may also play a role. In the northwest Mediterranean, inter-annual differences in the duration and onset of reproduction of round sardinella were related to temperature differences (Palomera and Sabatés, 1990). Moreover, Ben Tuvia (1960) noted that the gonad maturation of round sardinella begins at sea temperatures greater than 20 °C and Ettahiri et al. (2003) also related the spawning of round sardinella with high water temperatures. The process of gonad maturation and spawning in round sardinella may, however, be delayed due to unfavourable feeding or environmental conditions (Quaatey and Maravelias, 1999). Due to the flexible strategy that results from its demographic plasticity (Cury and Fontana, 1988) and its wide geographical range, round sardinella might be a model species for understanding climate change-mediated effects on fish populations.

The reproductive period of round sardinella in the present study was short and lasted two months. Indeed, the breeding season of fishes inhabiting environments with pronounced seasonal climatic variations is almost invariably confined to a brief and specific period of the year (Bye, 1984). The duration of spawning of round sardinella might be short due to the presence of the sympatric clupeoids, the European anchovy, *Engraulis encrasicolus* (Linnaeus, 1758) and European sardine, *Sardina pilchardus* (Walbaum, 1792) in the northern Aegean Sea. Increased antagonism occurs among clupeoid fishes at certain stages of their life cycles (Palomera and Sabatés, 1990), which has caused the evolution of different reproductive strategies to avoid antagonism in early and more vulnerable life stages (Wang and Tzeng, 1997). The temporal succession (Caragitsou et al., 1997, Wang and Tzeng, 1997) and spatial segregation (Palomera and Sabatés, 1990) of sympatric clupeoid larvae reduces competition for habitat and maximizes resource utilization (Wang and Tzeng, 1997).

The duration of round sardinella’s spawning is more extensive in the southern Mediterranean Sea (Tunisia, Egypt, Algeria, Libya: Table 2) and is probably attributed to the warmer climate compared to that of the northern Aegean. In other areas of its distribution (Table 2), the reproduction of round sardinella is highly variable regarding the time and duration of spawning. Consequently, its reproduction lasts throughout the year off the north-west African coast (Fontana, 1969), exhibiting intra-annual varia-

<table>
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<tr>
<th>Area</th>
<th>Months</th>
<th>Lₕ₀ (mm)</th>
<th>Fₐ (x10³)</th>
<th>Fₕ</th>
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<tr>
<td>Aegean 2001</td>
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<td>155.0 (M), 168.3 (F)</td>
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<td>197</td>
<td>-</td>
<td>-</td>
<td>0.99</td>
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tions with one (Fontana, 1969), two (Cury and Fontana, 1988), or even three (Quaatey and Maravelias, 1999) peaks of reproductive activity.

Size at maturity

Round sardinella males in the northern Aegean Sea were smaller and younger at maturity than females. Indeed, in short-lived species, maturation usually occurs at the end of the first year of life (Beverton, 1963). Bimaturism, which is common in species with promiscuous mating, external fertilization and indeterminate growth (Stearns, 1992), is also observed in other round sardinella populations (Quaatey and Maravelias, 1999; Gaamour et al., 2001). In general, higher L50 values have been reported for Atlantic stocks of round sardinella (Venezuelan waters, Ghana waters: Table 2). In the Mediterranean, however, round sardinella reaches sexual maturity at a smaller size (Table 2). Age and size at maturity vary among closely related species, among populations within species and among individuals within populations, suggesting that they can respond rapidly to natural selection (Stearns, 1992).

Size and age at first maturity depend on environmental and genetic factors (Wootton, 1998; Sampson and Al-Jufaily, 1999), but can be influenced by other factors such as long-term fishing pressure (Jennings et al., 2001). The latter may pose a severe impact on size at maturity forcing the population to mature at a smaller size in order to ensure the survival of the species (Olsen et al., 2004).

The L∞/L∞ ratio is generally smaller for large-sized species and larger for small-sized ones (e.g. Beverton, 1963; Longhurst and Pauly, 1987), which is also true for the Mediterranean fishes (Tsikliras et al., 2005a). The L∞/L∞ ratio for a dataset of 24 Hellenic marine fish species ranged between 0.33 and 0.74 with a mean value of 0.48 (Stergiou, 2000). The computed value for round sardinella ranks the species within the reported range and close to the maximum value. Beverton (1963) reported a range of ratios between 0.62 and 0.80 for clupeids, and a value of 0.65 for Sardinella spp., which agrees closely with the value calculated in the present study.

Fecundity and oocyte diameter

The absolute fecundity (FA) of round sardinella in the northern Aegean Sea exhibited high variability among individuals of the same size. This can be the result of either genetic differences among the females, or environmental conditions or a combination of both (Stearns, 1992; Wootton, 1998). The fecundity of round sardinella in the northern Aegean is close to the lower limit of the range reported so far for the species in both the Mediterranean and Atlantic Seas (Table 2). An important parameter accounting for these differences is the maximum recorded length in these areas, which is lower in the northern Aegean (max L=248 mm) when compared to the northwest African coast (max L=410 mm; Pham-Thuoc and Szypula, 1973) and southern Mediterranean (max L=292 mm; Bensahla Talet et al., 1988), the reason being that FA is a function of length (e.g. Wootton, 1998). However, on a unit body mass basis, the above differences were balanced. Thus, in Algerian waters relative fecundity (F∞) ranged between 246 and 933 oocytes/g, which is very close to that of the northern Aegean (Table 2).

The mean F∞ in the present study was strongly correlated with length and weight. The positive correlation of F∞ with length has been reported for round sardinella populations in the Mediterranean (Bensahla Talet et al., 1988; Gaamour et al., 2001) and the eastern Atlantic (Pham-Thuoc and Szypula, 1973). The parameter b of the relationship between F∞ and length is higher than those reported for round sardinella in Tunisian waters (Gaamour et al., 2001) and lies close to the upper limit of the previously reported values for other fishes (Wootton, 1998). The reproductive potential, as reflected in the increase in F∞ with length, indicates that round sardinella allocates more energy to reproduction as it grows. This is supported by the asymptotic decline of round sardinella’s growth with age (Tsikliras et al., 2005b). Such trade offs are common in fish, with the trade off between growth and present reproduction being potentially significant because female fecundity is a function of body size (Wootton, 1998). Besides body length and weight, which largely determine the fecundity of fish (see also Trippel and Neil, 2004; Tsikliras et al., 2005a), the physiological condition of maternal stock, expressed as total lipid energy, is also very important in estimating the number of eggs produced and predicting the subsequent recruitment (Marshall et al., 1999).

The frequency distribution of oocyte diameter indicated that, besides the permanent stock of primary oocytes, the oocytes of round sardinella in the northern Aegean Sea developed synchronously,
which is also the case for round sardinella in Libyan waters (Pawson and Giama, 1985). Although the frequency distribution of oocyte diameter is an indicator of the nature of spawning in fishes and the presence of more than one group of yolked eggs is an accepted criterion that more than a single spawning takes place (Blaxter and Hunter, 1982), further histological examination of the gonads and hormonal profile studies are required to ensure the single batch spawning of the species.

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